

Application of the phylogenetic species concept: A botanical monographic perspective.

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Summary

Snow, N. (1997). Application of the phylogenetic species concept: A botanical monographic perspective. *Austrobaileya* 5(1): 1–8. The diagnosis of phylogenetic species and infraspecific taxa is considered from the perspective of botanical monography. Diagnosing phylogenetic species using population aggregation analysis (PAA) cannot be done in the herbarium, as it is a population-based procedure. However, herbarium specimens can be aggregated into phylogenetic species based on the presence of fixed characters, and PAA methodology in the field is encouraged to the maximum extent possible. The importance of diagnosing phylogenetic species by ordinary morphological means is stressed. A species is thus an aggregation of sexual or asexual semaphoronts consistently diagnosable by a fixed character or combination of characters recognizable by ordinary morphological means. Application of this species definition will generally decrease species numbers in botanical monographs and could therefore overlook significant but non-fixed phenetic variation. Given the widespread existence of such variation it is concluded that the recognition of infraspecific taxa remains desirable. However, since varieties are explicitly subordinate to subspecies in the Code and imply hierarchical pattern where none is expected to exist, the recognition of only one infraspecific category is recommended.

Keywords: phylogenetics, phylogenetic species, species concepts, subspecies, varieties, botany, monographs.

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We need good theoretical contexts in which to formulate operational interpretations in order to proceed with empiricism. – Estabrook (1972).

Introduction

In the current phylogenetic era the histories of biological lineages have become of paramount importance for interpreting biological pattern and process. The impact of phylogenetic thinking has necessitated a critical re-evaluation of every important concept in systematics (Davis 1995; Harvey et al. 1996; Snow 1996).

For example, the phylogenetic perspective has spawned the concept of phylogenetic species (Nelson & Platnick 1981; Cracraft 1983, 1989; Donoghue 1985), the definition and identification of which have been controversial (Nixon & Wheeler 1990;

de Queiroz & Donoghue 1990b; Wheeler & Nixon 1990). One debate has surrounded 'history' versus 'character' based approaches for diagnosing phylogenetic species (Mishler & Brandon 1987; de Queiroz & Donoghue 1988; Nelson 1989; Nixon & Wheeler 1990; de Queiroz & Donoghue 1990a,b; Baum & Donoghue 1995; Luckow 1995). A second debate has been whether phylogenetic species must be monophyletic (see Crisp & Chandler 1996).

Another recent idea originating from the phylogenetic perspective is a methodological approach by which phylogenetic species can be recognized (Davis & Manos 1991; Davis & Nixon 1992). Termed 'population aggregation analysis' (henceforth PAA) and formulated largely in the context of isozyme data, PAA

tabulates populations for the presence or absence of characters and then iteratively aggregates these populations based on whether characters have gone to fixation (Davis & Nixon 1992; Davis & Goldman 1993).

McDade (1995) recently provided a detailed review of the monographic literature regarding species concepts and their application in practice (see also Hamilton & Reichard 1992). Although other botanists have considered the species problem from the phylogenetic perspective (Crisp & Weston 1993; Crisp & Chandler 1996), only two monographs cited by McDade (1995) (Soreng 1991: 508; Luckow 1993: 38) explicitly used a phylogenetic species concept *sensu* Nixon and Wheeler (1990). To the best of my knowledge, no papers published after the period covered by McDade (1995) addressed either the application of population aggregation analysis (Davis & Nixon 1992) using morphological characters, or the recognition of phylogenetic species in the herbarium. In addition, with the exception of Soreng's (1991) detailed rationale, the issue of recognizing infraspecific taxa under a phylogenetic species concept largely has been overlooked (Luckow 1995).

Having recently completed a phylogenetically-based monograph of the grass genus *Leptochloa* P.Beauv. (Snow 1997) using standard approaches (herbarium, field, greenhouse), I had to consider two issues relevant to the botanical monographer: 1) how to diagnose phylogenetic species relying mostly on herbarium specimens using morphological characters, and 2) the theoretical and pragmatic considerations of whether to recognize infraspecific taxa. I here outline the rationale I followed, and which others may wish to follow, in the hope of stimulating further discussion on these topics.

Phylogenetic species and their recognition in botanical monographs

Under a phylogenetic perspective a monographer may wish to use a phylogenetic species concept (hereafter 'PSC') (Cracraft 1983, 1989; Donoghue 1985; Nixon & Wheeler 1990). A phylogenetic species has been defined

as 'the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)' (Nixon & Wheeler 1990). Contrary to some views (de Queiroz & Donoghue 1988; Vrana & Wheeler 1992), it has been argued that the terms monophyly and paraphyly are not applicable at and below the species level (Nixon & Wheeler 1990; Davis & Nixon 1992). This follows the reasoning of Hennig (1966) that only entities expected to have hierarchical relationships, and not tokogenetic relationships, should be included in cladistic analyses.

An influential paper of Du Rietz (1930: 347) foreshadowed the need for population-based sampling as a necessary empirical antecedent of forming species boundaries. Population aggregation analysis (Davis & Nixon 1992) is not the first time that fixation of characters has been deemed necessary for the recognition of taxa (Davis & Heywood 1973: 78), nor is it the first methodological procedure linked directly to a particular species concept. As the best known example, gene flow and reproductive isolation are linked to the biological species concept, but these criteria are now rarely used in practice to diagnose species boundaries and are thus essentially non-operational (Whittemore 1993; Brookes 1996). In contrast, PAA provides precise methodological criteria by which phylogenetic species can be diagnosed, and in many cases it will be highly operational (but see below). Within the assumptions of the phylogenetic paradigm the logic and methodology of PAA is internally consistent. In many cases, however, the herbarium systematist will be able to apply PAA only under certain constraints.

One constraint of applying population aggregation analysis is that, with the exception of small genera that occur in relatively close proximity to the monographer, PAA will often be logistically infeasible. This is particularly true for species-rich genera and those with intercontinental distributions. Few researchers have adequate time or funding for the necessary travel and intensive population sampling mandated by a strict adherence to PAA methodology. These realities acknowledged,

monographers probably should collect using PAA methodology to the maximum extent possible; that is, sample multiple genotypes for a given population. This is particularly true for problematic species that appear to lack fixed characters or combinations of characters. The data collected from multiple genotypes in a population (hence, independent samples) are systematically informative because they permit analysis of intrapopulational variation, even if its evaluation is non-statistical. Such data are a critical consideration under the phylogenetic species concept, since fixed characters (100% occurrence) at the population level provide the basis by which phylogenetic species are recognized (Crisp & Chandler, 1996). For the herbarium taxonomist, however, the analysis of intrapopulational variation generally has been possible only when species were known from a single locality (e.g., tropical genera such as *Cryptanthus* Otto & A. Dietr. or *Anthurium* Schott.; see Appendix 1).

The second constraint regarding the recognition of phylogenetic species bears on what can happen when the PSC is pushed to its reductionist or aggregationist limits. The use of fixed characters to recognize phylogenetic species may increase (Cracraft 1992) or decrease (Davis & Nixon 1992) the total number of species recognized. As previously argued (e.g., Olmstead 1995), a species could be recognized at the reductionist extreme on the basis of a single fixed nucleotide base pair. However, such a species would not be recognizable by ordinary means. A potential problem at the aggregationist extreme could be the lumping of multiple but phenetically distinct entities due to the absence of any fixed character(s) (see below). Those working with large tropical groups will be keenly aware of this potential problem. An aggregationist extreme also could overlook at least two important considerations in plant biology: 1) the existence of morphological outliers resulting from developmental abnormalities, which are not infrequent in plants, and 2) intermediates due to interspecific hybridization. However, biological reality does not reside within agarose gels or overly rigid theoretical constructs. Meaningful phylogenetic species, to the herbarium systematist, the ecologist,

and the community at large, must be those diagnosable by 'ordinary means' (Cronquist 1978). Thus, the second constraint of PAA methodology is that the monographer must recognize phylogenetic species using ordinary morphological means. To the botanical monographer, a phylogenetic species is an aggregation of sexual or asexual semaphoronts consistently diagnosable by a fixed character or combination of characters recognizable by ordinary morphological means. Users of herbarium-based monographs must realize, however, that additional but cryptic lineages may exist within morphologically based species. In *Leptochloa* an example would be the tetraploid, hexaploid, and octoploid levels occurring in the neotropical species *Leptochloa dubia* (Nees) Kunth (Gould 1975; Snow 1997).

Given the inability to always adhere strictly to the methodology of PAA, yet acknowledging the decided preference for phylogenetic species diagnosable by ordinary means, the best option for the botanical monographer to approximate the recognition of phylogenetic species in the herbarium is to search for a fixed character or suite of characters by which a species can be consistently recognized. The emphasis on fixed (versus polymorphic) characters derives from the fact that only fixed characters are capable of reliably suggesting that the relationships between taxa bearing them will be hierarchical, a necessary assumption of cladistic methodology (Hennig 1966; Davis & Nixon 1992; Doyle 1995). Fixed characters need not be qualitative; quantitative characters showing consistent gaps (and not merely differences in mean values) are also admissible diagnostic features (Thiele 1993; Luckow 1995). The monographer can thus aggregate herbarium specimens into phylogenetic species based on fixed characters observable by ordinary means. This approach is nothing new in monography, other than perhaps the requirement of character fixation. Differences of opinion regarding what constitutes 'ordinary means' will surely exist, but I see no reason to exclude characters that require up to 30x magnification, which is readily available in most herbaria. The aggregation of specimens based on character fixation is a repeatable and testable approach

(Snow 1996) that allows future workers to test hypotheses of species circumscription. With this approach a phylogenetic species is what the data (i.e., the characters) warrant, not merely what a competent systematist says it is.

Using the criteria for recognition of phylogenetic species outlined above, my revision of *Leptochloa* resulted in a decrease in species number (Snow 1997). Application of the PSC using field and herbarium data required merging the Australian taxa formerly known as *Leptochloa ciliolata* (Jedw.) S.T.Blake, *L. decipiens* (R.Br.) Stapf ex Maiden, and *L. peacockii* (Maiden & Betcher) Domin (Lazarides 1980; Stanley & Ross 1989; Wheeler et al. 1990; Simon 1993) into a single species (Snow 1997). The necessity to lump occurred despite the fact that three readily distinguishable entities can exist in considerable numbers sympatrically within a few metres and maintain attributes which, *in that locality*, make them diagnosably distinct (Snow pers. obsv.). However, the attributes by which these taxa have been recognized can also break down in the field (Snow pers. obs.), and significant numbers of intermediates exist as herbarium specimens. Thus, whereas populations can be locally distinct, they may not be globally distinct. Since locally distinct populations not globally fixed for a character or combination of characters still probably reflect underlying genetic variation, it becomes necessary to consider whether infraspecific taxa should be recognized.

The recognition of infraspecific phylogenetic taxa in botanical monographs

Theoretical considerations of infraspecific taxa have been largely overlooked during discussions of species concepts rooted in the phylogenetic paradigm (Luckow 1995). Many (Stebbins 1950; Wilson & Brown 1953; Grant 1981; Mayr 1982) but not all (Du Rietz 1930; Raven 1962; Raven & Raven 1976) pre-cladistic discussions of infraspecific taxa were linked to the 'biological' species concept, or BSC. Reproductive isolation and gene flow, the central tenets of the BSC (Whittemore 1993), cannot be invoked under the phylogenetic paradigm, given its different

assumptions (Luckow 1995). If they are to be recognized, phylogenetic subspecies or varieties, like their 'biological' counterparts, probably will lack consistent criteria for their recognition (Darwin 1859; Grant 1981; but see Pimentel 1959).

Although cladistic approaches are routinely used by population geneticists below the species level to trace gene genealogies (Avice 1989; Crandall & Templeton 1993; Doyle 1995; Maddison 1995; Moritz & Hillis 1996), for the botanical monograph and the phylogenetic analyses on which the supraspecific groups will be based, phylogenetic species are the minimal units of cladistic analysis. However, that does not necessarily make phylogenetic species the minimal taxa. It is possible to formally recognize phenetic taxa below the species level which, unlike phylogenetic species, are not expected to be hierarchically related. This seems particularly defensible if the monographer has field experience with the group, since variation easily detected in the field is frequently not captured on pressed herbarium specimens. For example, in the orchid genus *Cryptocentrum* Benth., leaf phyllotaxis (spiral/distichous), inflorescence position (erect/pendant), and floral bracts (spathaceous/tubular) are diagnostic and fixed characters readily observable in the field, yet are cryptic on herbarium sheets (G. Carnevali pers. comm.).

Returning to the earlier example of *Leptochloa*, application of the phylogenetic species necessitated lumping *L. ciliolata*, *L. decipiens*, and *L. peacockii* into one species. However, given that 1) others have recognized three phenetic entities (Simon 1993; Stanley & Ross 1990); 2) these phenetic entities can be diagnosably distinct sympatrically (Snow pers. obs.); but that 3) their distinctness can also break down in the field (Snow, pers. obs.), I recognized a single species with three subspecies (Snow 1997, in press). Infraspecific taxa can thus be phenetic groupings that presumably reflect genetically-based variation, but the patterns of which are non-fixed and non-hierarchical. Under this approach an infraspecific taxon will still be what a

competent systematist says it is (Hubbell 1954: 120; Hedberg 1957: 14; Raven 1962: 6), although one would hope that newly recognized infraspecific taxa would still be supported with evidence (narrative comment or numerical data) of some sort (Hedberg 1957: 16). My view of infraspecific taxa as phenetic clusters that reflect underlying genetic variation is similar to the species concept outlined by Crisp and Weston (1993), except at a lower taxonomic level.

A question arises then regarding phenetic pattern: Should we formally recognize such pattern at the infraspecific level if it becomes badly blurred or non-diagnosable in a global context? In other words, should an infraspecific taxon be named if the taxonomic placement of some (or all) of its members requires knowledge of their geographical occurrence (du Rietz 1930; Stebbins 1950; Brown & Wilson 1954; Pimentel 1959; Mayr 1982)? For highly vagile organisms, such as the many *r*-selected annual species of *Leptochloa*, it is unreasonable to expect that infraspecific variants will always be restricted to a particular geographic domain (e.g., Snow & Simon in press). Characters, fixed or non-fixed, are heritable and emergent properties of populations or series of populations. Geographical distribution is not a heritable feature and does not necessarily reflect distinct genetic lineages, although it may reflect genetic variation. The actions of mutation, selection, drift, and lineage sorting collectively predict the existence of geographically localized variation in widespread species. If a putative infraspecific taxon cannot be distinguished independent of its geographical occurrence—that is, if no combination of non-fixed characters exists by which a ‘specimen’ can be identified at the infraspecific level—then that taxon should not be recognized. Geographical distribution by itself is an invalid criterion for recognition of infraspecific taxa.

Finally, the monographer must consider how many infraspecific ranks should be recognised. The International Code of Botanical Nomenclature (Greuter et al., 1994) allows for names at two infraspecific ranks: subspecies, and at a subordinate level, varieties. However,

even one infraspecific level of non-fixed phenetic pattern implies fuzzy boundaries between the constituent infraspecific taxa. Under the phylogenetic species concept it is illogical to recognize more than one level of phenetic infraspecific pattern, since variety is subordinate to subspecies, and if both were recognized, it would imply hierarchical pattern where none was expected to exist (Nixon & Wheeler 1990). Complex patterns of variation can certainly occur (Gould & Johnston 1972; Thorpe 1983; Crisp & Chandler 1996), but those inclined to recognize both subspecies and varieties under a phylogenetic species concept using ordinary means might consider whether they are attempting to recognize a degree of *hierarchical* pattern that does not really exist. As noted by others, the recognition of more than one infraspecific rank generally engenders confusion, especially to the non-specialist (Stebbins 1950: 32-33; Hedberg 1957: 15). With these considerations in mind it seems most appropriate to formally recognize only one infraspecific category.

Conclusions

I agree with earlier views (Davis & Goldman 1993; Kellogg 1994; McDade 1995; Luckow 1995) that monographers should clearly outline their species concepts and methodological approaches so that future workers can improve upon extant taxonomies as additional data warrant. Otherwise, successive revisions are merely a chronological array of untestable opinions which, even if based on reliable data, are difficult to evaluate. The exposition presented here represents my own attempts to integrate and pragmatically apply recent theoretical advances in systematics to the writing of a botanical monograph (Snow 1997).

Phylogenetic species are the minimal units amenable to cladistic analysis for the purposes of botanical monography in the phylogenetic perspective. A phylogenetic species is an aggregation of sexual or asexual semaphoronts consistently diagnosable by a fixed character or combination of characters recognizable by ordinary means. A single infraspecific level of non-fixed phenetic variation may be recognized taxonomically

provided the variation is not irretrievably obscured when the species is viewed globally. For the recognition of phylogenetic species fieldwork should focus on the population sampling of separate genotypes for poorly known species, and the populations evaluated using PAA to the maximum extent possible.

The methodology outlined here is not meant to be critical of earlier work. Others will find much to disagree with regarding the logic and rationale outlined above for recognizing species and infraspecific taxa for a phylogenetically-based monograph. However, if this article stimulates further dialogue regarding these topics, particularly in the context of producing scientifically meaningful but useful botanical monographs, it will have served a useful purpose.

Acknowledgements

I thank the following for discussions regarding the ideas contained herein: J. Bradford, G. Carnevali, T. Croat, J. Davis, W. Hauk, P. Hoch, S. Malcomber, I. Ramírez, and P. Raven. The comments of an anonymous reviewer were helpful. My research has been supported by the Missouri Botanical Garden (Andrew W. Mellon Foundation), a grant from the National Science Foundation to the Plant Biology Program at Washington University (St. Louis), and the National Geographic Society (NGS 5594-95).

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Appendix 1. The sampling of numerous genotypes from multiple populations could quickly result in curatorial problems for a given institution. To alleviate curatorial congestion, I suggest a separate collection number be assigned to each genotype and that specimen labels clearly reflect the genotypic uniqueness of each specimen. For example, a numbering scheme for a given population might be *Collector et al.* 7249-A, *Collector et al.* 7249-B, etc., with a statement on the label

reading "Each letter designates a different genotype". Upon completion of the monograph *n*-1 genotypes from each population could be distributed to other herbaria following standard procedures. An indication on the labels of the herbaria to which duplicates will be distributed would assist future workers. Given its relative ease collectors should also consider collecting fresh leaf material suitable for molecular studies in silica gel.